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Population responses of common carp *Cyprinus carpio* to floods and droughts in the Pampean wetlands of South America

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Abstract

Common carp (*Cyprinus carpio*) is a global invader that exhibits a wide distribution in Argentina, particularly in shallow lakes and wetlands of the Pampean region. The hydrological conditions of these environments are driven by variations in annual precipitation that determine inter annual changes in water levels leading to flood-drought cycles. The present study focused on understanding the *C. carpio* population responses to annual rainfall regime and long-term flood and drought events in the Ajó wetlands located in the east of the Pampean region. The results of a two-year biological sampling program showed that *C. carpio* feeding rate, reproduction, condition, and recruitment were associated with the hydrological cycle. Otolith derived age structure of the population and back-calculated recruitment strength revealed that extraordinary flooding events generated strong cohorts while dry years resulted in low recruitment. Its long-life span (maximum 14 years in Ajó) coupled with a high fecundity, and broad diet allows *C. carpio* to persist in refugia during dry years and capitalize on wet years when inundation of the floodplain enhances recruitment and facilitates spread. Management and control strategies for this invader should therefore incorporate hydrological variability by promoting intensive removal campaigns during dry years when populations are dominated by large fish confined in remnant water-bodies and, during wet years, carp harvest fisheries should be promoted to reduce population density when increased connectivity is likely to facilitate spread.

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Keywords
Cyprinus carpio, exotic species, recruitments dynamics, Pampean region

Introduction

Common carp *Cyprinus carpio* Linnaeus, 1758 is a freshwater fish native to the Ponto-Caspian region (Balon 2004) that, as a result of human introductions, has invaded freshwater ecosystems on all continents except Antarctica (Zambrano et al. 2006; Vilizzi et al. 2015). The invasive success of *C. carpio* is strongly related to its high tolerance to environmental stress (e.g. Edwards and Twomey 1982; Weber et al. 2010; Maiztegui et al. 2016); a generalist feeding strategy (Sibbing 1988; Colautti and Remes Lenicov 2001; García-Berthou 2001); fast growth, high fecundity and early sexual maturation (Panek 1987; Winker et al. 2011; Vilizzi and Copp 2017). Impacts are linked primarily to their bottom grubbing feeding mechanism which mobilizes sediments, increases turbidity and enhances nutrient availability which have been shown to alter aquatic food webs on multiple trophic levels (Vilizzi et al. 2015). As a result, *C. carpio* is considered to be one of the most pervasive and destructive of freshwater fish (Koehn 2004; Matsuzaki et al. 2009; Kloskowski 2011) and is listed amongst the world's worst 100 invasive alien species (Lowe et al. 2000) therefore controlling *C. carpio* populations is a high priority in many countries. Examples include legislative limitations to movement in South Africa (Ellender et al. 2014), viral biocontrol in Australia (McColl et al. 2018), and direct control using piscicides in the USA (Meronek et al. 1996; Bajer et al. 2009). Although approaches differ between regions and countries, it is widely accepted that an understanding of the biology and population dynamics of *C. carpio* in the invaded environment is critical to the efficacy of control measures (Driver et al. 2005; Bajer et al. 2012; Weber and Brown 2013; Koehn et al. 2017).

In Argentina, *C. carpio* were introduced for ornamental and aquaculture purposes in the second half of the 19th century and the species is currently distributed throughout the center and north of the country (Baigún and Quirós 1985; Maiztegui et al. 2016). In an assessment of environmental suitability, Maiztegui et al. (2016) concluded that more than half of the country, and especially the Pampean region, offered suitable climatic conditions for its establishment. Indeed, in this region *C. carpio* have expanded their distribution over the past 30 years and now occupy many eutrophic and vegetated shallow lakes. Pampean lakes provide considerable ecosystem services that include a valuable recreational fishery for native species (Baigún and Delfino 2003), but are subject to multiple stressors including catchment degradation, habitat modification by man-made infrastructure and species invasions (Baigún and Lombardo 2017). *Cyprinus carpio* are of particular concern as impacts on shallow lakes and floodplains are well-documented (Lougheed et al. 1998; Vilizzi and Tarkan 2015; Huser et al. 2016). Key to the effective management of *C. carpio* is understanding its population dynamics in invaded environments (Driver et al. 2005; Bajer et al. 2012; Weber and Brown 2013; Koehn et al. 2017).

In this study, the Ajó wetlands, located in the eastern Pampean region, were used as a natural experiment to assess how *C. carpio* populations respond to short and long-

term variations in inter annual flood-drought cycles. The Pampean region is characterized by the presence of irregular periods of persistent droughts, interspersed with periods of heavy rainfall that cause severe floods, as happened for example in 1980, 1985, 1993 and 2002 (Scarpati et al. 2011; Scarpati and Capriolo 2013). The hydrological dynamics of the wetlands and their shallow lakes are complex as they are linked to macro-scale episodic events such as El Niño and La Niña events (ENSO) (Bohn et al. 2016; Elisio et al. 2018), and to meso-scale climatic phenomena such as the South American low-level jet stream (Virji 1981), the South American monsoon (Zhou and Lau 1998) and the South American Convergence Zone (SACZ) (Barros et al. 2000). The retraction or expansion of water surface area in the Pampean wetlands is therefore dependent on the intensity and duration of these rainfall events, which in turn affect both the structure and abundance of Pampean fish assemblages (Colautti et al. 2015) and the expansion of alien species including *C. carpio* (Maiztegui et al. 2016).

One of the major areas occupied by *C. carpio* in this region is the Ajó wetlands, a complex and highly variable hydrologic system where *C. carpio* dominate the ichthyofauna both numerically and in biomass (Maiztegui 2016). This study is aimed at understanding how seasonal and inter-annual hydrological variations influence *C. carpio* biological responses and how extraordinary flooding years affect recruitment.

Methods

Study area

Fieldwork was carried out in the Ajó wetlands (36°36.89'S; 57°06.69'W), which are located in the east of the Pampean region (Fig. 1). According to the classification of Thornthwaite (1948), the climate is sub-humid to humid, mesothermal and with scarce to null water deficiency (Carol 2008). Annual average temperature is 15.2 °C and mean annual precipitation is 1078 mm y^{-1}, with 1634 and 421 mm y^{-1} being the maximum and minimum registered between 1887 and 2002, respectively (Carol 2008). Rainfall is seasonal with peaks during the austral spring and summer (Carol 2008). Hydrologically, the area is a complex and heterogeneous system that includes an estuarine brackish water zone and an inland freshwater zone. In the estuarine zone, the Ajó River is the main natural water course that drains into the Río de la Plata estuary (200 km from Buenos Aries City). The main water courses of the freshwater portion are Canal Dos (C2) and Canal el Palenque (CP) (Fig. 1), which are floodgate regulated man-made drainage canals for de-watering flooded lands during high rainfall conditions affecting the Ajó River. Both canals comprise a complex network of small creeks with semi-permanent water that are temporarily connected depending on water levels (Carol 2008). The floodgates are generally closed to prevent the inflow of brackish water from the Ajó River estuary, retaining freshwater in the wetlands regulating the flows towards the bay depending on the hydrologic period in the area (Carol et al. 2012; 2013).

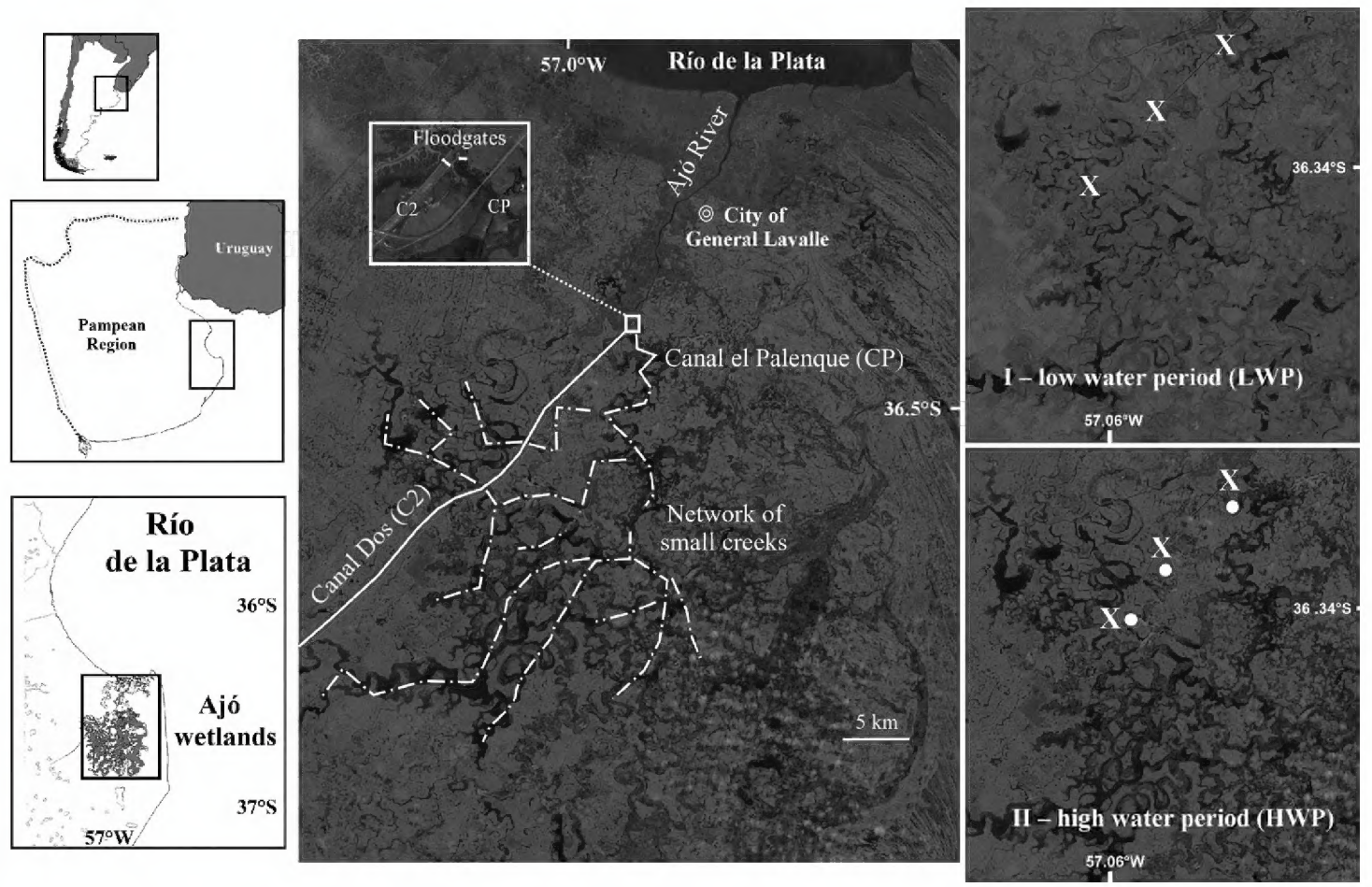

Figure 1. Geographical location of the Ajó wetlands in the Pampean region, indicating the main water courses: Ajó River, Canal Dos, Canal el Palenque (with detail of their respective flood gates) and the main streams of the network of small creeks. Satellite images from the Ajó wetlands during two contrasting hydrological scenarios: **I** low water period (LWP), sampling sites in Canal Dos (X) **II** high water period (HWP), sampling sites in Canal Dos (X) and the network of small creeks (white circle).

During drought periods, water levels in the C2 and CP are reduced and the network of small creeks becomes dry; meanwhile, during floods, the mean depth of the Ajó wetland increases up to 2.5 m (Carol 2008). In intermediate periods, the water level of the network of small creeks undergoes a periodic and unstable hydrologic pattern, connecting or disconnecting with the canals depending on the annual precipitation and evapotranspiration regime and the retained water in the wetland.

Water level periods and sampling program

Sampling was conducted monthly from April 2009 to March 2011. This included low water periods (LWP) from April to June 2009 and January to February 2010 during which water levels at the network of small creeks were below 0.2 m, and high water periods (HWP) from July to December 2009 and from March 2010 to March 2011 when the water level of these environments was above 0.2 m. During LWP *C. carpio* specimens were sampled only from C2 (Fig. 1I) but during the HWP they were collected in C2 and also in the network of small creeks (Fig. 1II). Monthly water balance was calculated as the difference between precipitation records provided by the mete-

orological station located in the city of General Lavalle (P) and the historic monthly evapotranspiration regime (EVT) (Carol et al. 2015).

Fish were collected using fyke nets (Colautti 1998) with a 5 mm mesh end, 1.2 m wide × 0.8 m deep opening, and a 0.8 m height × 20 m long guiding net. In addition, a 70 m long beach seine with a 35 mm bar mesh was used. Fyke nets were deployed at night while seine netting was conducted during the day; it is important to note the use of these fishing gears was applied with the aim to encompass the maximum possible range of L_T for *C. carpio*. All captured fish were measured (L_T, nearest mm) and weighed (W_T, nearest g). The total length frequency distribution (L_T) of each fishing gear was contrasted by means of the non-parametric *Kolmogorov-Smirnov* test. Monthly, a maximum of 40 specimens (L_T > 350 mm) were euthanised by severing the spinal cord and the asteriscus otoliths were removed and stored dry. The mass of the gonads (W_G, g), digestive tract (W_{DT}, g) and the eviscerated body (W_S, g) were obtained for each fish. The foregut (i.e. portion between the esophagus and the first major bend of the digestive tract) was then dissected out and the degree of fullness (DF) assessed according to the subjective scale recommended by Hyslop (1980) as either: empty (0), 1/3 full (1), 2/3 full (2) or full (3). Gut contents were preserved in buffered 10% formalin for later diet composition analysis.

Reproduction and condition

To describe the gonadal cycle and determine the length of the spawning season, the gonadosomatic index (GSI) was calculated as $GSI = W_G / W_T * 100$, and assessed within the context of water level (m) and temperature (°C) measured at C2. The relative condition factor (K_N: Le Cren 1951) was calculated as: $K_N = W_T / W_P$, where W_P is the length-specific mean weigh predicted by the population's W_T and L_T relationship and regressed against the monthly water level variation.

Gut contents

The repletion index (RI), calculated as $RI = W_{DT} / W_S * 100$, was used to determine monthly variation in feeding intensity throughout the study period. In the laboratory, monthly samples were assessed for diet composition. To this end, foregut contents were homogenized with a magnet shaker, and a sub-sample of 1 ml obtained by means of a pipette. This sub-sample was evaluated and analyzed under a stereomicroscope (Olympus SZ61, ×2) in a Sedgwick-Rafter (APHA 1995) counting chamber. Consumed items were discriminated based on their origin (vegetal or animal). In the case of vegetal material, it was possible to differentiate between vegetal debris and remains of seeds; whereas animal items were classified into major taxonomic categories. All identifiable items were then quantified volumetrically through a graduated measuring capsule (Hellawell and Abel 1971; Hyslop 1980) and this procedure was performed

in triplicate for each stomach. Once all the dietary items were identified together with their respective volumes in the samples, their abundance was extrapolated to the rest of the known volume of the gut contents.

Average monthly values of RI and the percentages of DF assigned in each month (DF%) were plotted against time to determine annual variability in feeding intensity. In addition, analyses were also undertaken to assess for differences between samples obtained from C2 (LWP), C2 (HWP) and the network of small creeks, to assess whether site or water level influenced feeding intensity.

A General Linear Model (GLM) analysis was performed to assess the influence of water level, location and season (month) over RI. A Poisson distribution for response variable and logit-link function were used to develop the models. The adjustment of GLM parameters was evaluated using the Student's t-test.

In order to detect temporal trends in length structure and recruitment events during the sampling period, monthly L_T-frequencies distributions corresponding to each sample date were graphed in time sequence.

Ageing

Asteriscus otoliths (Vilizzi 2018) were embedded in clear epoxy resin blocks with their nuclei aligned and transversely sectioned along the dorso-ventral plane through the primordia using a cutting saw. Otolith sections (0.4 mm) were mounted on microscope slides and analyzed under a microscope using transmitted light by two individual readers without knowledge of the date of capture or fish length. The number of annuli was determined by counting the opaque zones along an aging transect from the nucleus to the edge of the ventral portion of the sectioned otolith (Brown et al. 2004). If age estimates between readers were identical, then the count of growth zones was accepted, but when they differed, a third reading was conducted.

As the rate at which growth zones are deposited in *C. carpio* otoliths can differ between localities (Winker et al. 2010) growth zone deposition rate in the Ajo wetlands population was validated using edge analysis (Campana 2001). To this end, the optical appearance of the edge of each otolith was assessed, and categorized as either optically opaque (1) or translucent (0) (Fig. 2). The proportion of otoliths with an opaque zone present at the edge was then arranged on a monthly basis, and the time of annulus formation was estimated using periodic logistic regression (See Winker et al. 2010).

Based on otolith readings and L_T measurements, an age-length key (ALK) for the *C. carpio* population under study was obtained (n = 177). The integrated L_T frequency distributions of the months of slow growth (according to edge analysis) for both years of sampling were transformed to age by means of the ALK, thereby obtaining two age structures for the population. These were analyzed to determine the mean relative representation of each year class (cohort) and then, based on the documented in-

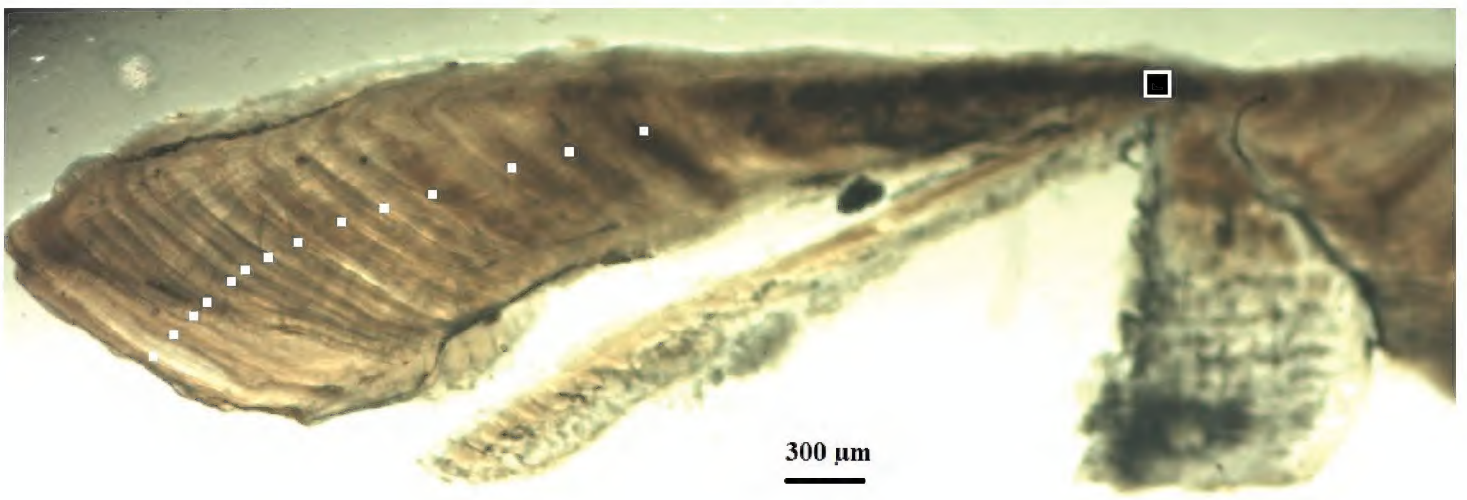

Figure 2. Photomicrograph of a sectioned asteriscus otolith, indicating the position of the nucleus (black square) and the marked annuli (white squares).

stantaneous natural mortality rate for *C. carpio* in Pampean region M = -0.784 yr^{-1} (Colautti 1997), the strength of each year-class was back-calculated as an estimator of each recruitment. Such calculation was obtained according to the following equation: $N_0 = N_t / e^{-0,784t}$, where N_0 is the number of individuals at time $t = 0$, N_t is the number of individuals at time t and t = years. To demonstrate the response of *C. carpio* population to hydroperiods, estimated annual recruitment were regressed against the respective yearly precipitations in the region (Diovisalvi et al. 2010; Colautti et al. 2015).

Results

Water level variation

The monthly water level variation of C2 and the network of small creeks is presented together with the hydrological balance regime (P-EVT), evidencing the alternation, duration and timing of hydrological scenarios LWP and HWP (Fig. 3). It is important to note that during the sampling period precipitation was considered average.

Sampling results and fishing gear selectivity

A total of 2363 fish measuring between 90 and 800 mm L_T and weighing between 12 and 6820 g W_T were sampled during the study. Fyke nets collected 414 *C. carpio* individuals (90–715 mm L_T) and the beach seine nets captured 1949 specimens (125–800 mm L_T). Although fyke nets sampled juvenile fishes more effectively, the length frequency distributions fish of ≥ 300 mm L_T did not differ between gears (*Kolmogorov-Smirnov*, $D = 0.09$; $p = 0.098$). Most fish (81.9%) were obtained from C2 and the remainder (18.1%) from the network of small creeks.

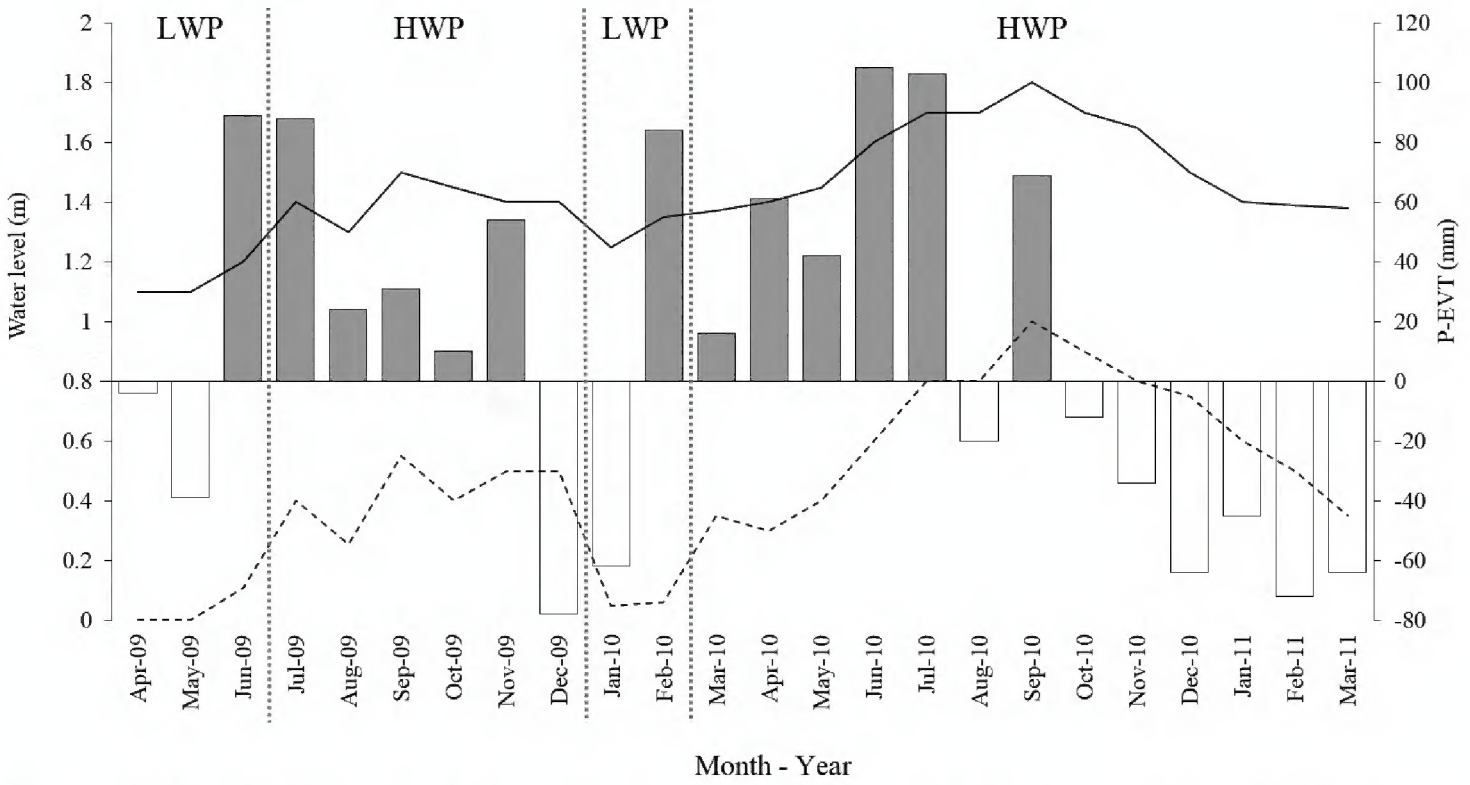

Figure 3. Monthly water level of Canal Dos (continuous line) and the network of small creeks (dotted line), indicating low water periods (LWP) and high water periods (HWP). Bars indicate the monthly water differences (mm) between precipitation (P) and evapotranspiration regime (EVT), grey bars represent months with hydrological excess and white bars represent months with hydrological deficit.

Reproduction

Female GSI values exhibited a wide range of monthly variation, showing a differential gonadal ripening through the study (Fig. 4a). Higher values of GSI were observed during the HWPs regardless of the year under consideration, but the development of GSI differed between years. During 2009, a seasonal pattern was observed whereby the average GSI values increased until reaching their maximum during early spring in concordance with water temperature of 16.3 °C. Thereafter, GSI decreased to a minimum in the late spring. In contrast, in 2010, two GSI peaks were noted, the first occurring in winter with water temperatures of 11.4 °C and the second in early summer at 23.3 °C (Fig. 4a).

Male GSI also showed wide monthly variation with peaks during autumn and winter (Fig. 4b). Differences between years were, however, not detected as clearly as with female fish. Male GSI typically increased during autumn (5–8) and winter (6–8) and decreased thereafter.

Gut contents

Cyprinus carpio feeding intensity (Fig. 4c) showed that they fed more actively during the months when the water levels were highest regardless of the season or year (Fig. 3). The 65% of analyzed digestive tracts (n = 112), corresponding to specimens with L_T that ranged between 400–800 mm, demonstrated that *C. carpio* had an omnivorous

Table 1. Diet of *Cyprinus carpio* in the Ajó wetlands: percent number in volume (Vol%) phylogenetically arranged, increasing in taxonomic complexity. Number of foreguts (n = 73, including specimens captured in Canal 2 during low water periods (n = 16), high water periods (n = 38) and in the network of small creeks (n = 19). Total volume of prey items = 20.45 ml.

Food categories	Vol%
Algae	1.9
Seeds	23.9
Plant debris	50.1
Rotifera	<0.1
Statoblasts of Bryozoa	<0.1
Remains of Mollusca	0.4
Copepoda	3.0
Cladocera	5.0
Ephipids of Cladocera	0.9
Ostracoda	0.9
Amphipoda	0.4
Decapoda	1.8
Remains of Crustacea	0.1
Larvae of Insecta	4.8
Remains of Insecta	0.5
Acari	<0.1
Remains of Arthropoda	5.4

diet with a broad trophic spectrum including both plant and animal prey (Table 1). In turn, the GLM analysis suggests that the RI was mainly influenced by the water level of C2 over location or time of the year, explaining 27 % of the RI variation ($p < 0.05$).

Changes in fish condition were closely linked to water level and feeding intensity, being detected the lower values of monthly average RI and K_N during LWP, and the higher values during HWP (Fig. 4.d). There was a positive linear relationship between the monthly K_N values and the water level in C2 ($y = 2.5804x - 1.2911$, $r^2 = 0.7138$). In addition, the analysis showed significant differences in K_N taking into account sites and water level periods (ANOVA, $F = 33.74$; $p < 0.05$), exhibiting fish from C2 (LWP) a lower K_N than C2 (HWP) and the network of small creeks ($p < 0.05$). During HWP, K_N did not differ between environments d ($p = 0.161$).

Monthly length structure

The structure of monthly length frequency distributions demonstrated that during 2009 the population consisted exclusively of adult specimens ($L_T > 350$ mm, Maiztegui 2016), and this was regardless of water level period or sampled location. In the summer of 2010, the length structure of the population experimented a change by inclusion of a large number of age-0 individuals ($L_T < 350$ mm) (Table 2; Fig. 5). This cohort

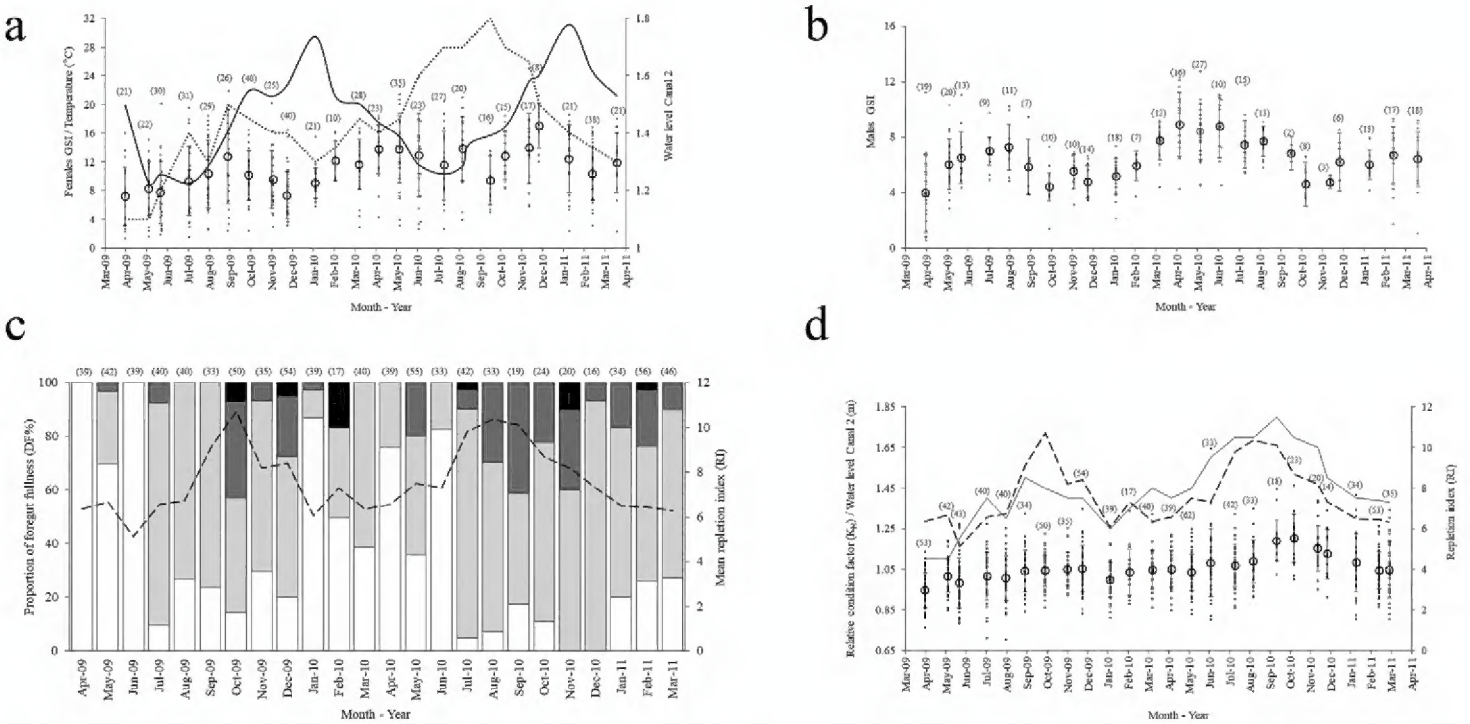

Figure 4. a Monthly changes in female GSI of *C. carpio*, presenting observed values (circles), mean (big circles) and standard deviations together with temperature (continuous line) and water level (dotted line). Numbers above (in parentheses) refer to the number of analyzed individuals in each month **b** Monthly changes in male GSI of *C. carpio*, presenting observed values (circles), mean (big circles) and standard deviations. Numbers above (in parentheses) refer to the number of analyzed individuals in each month **c** Monthly degree of fullness proportion (DF%) of *C. carpio*: white bar = 0 (empty), light grey bar = 1 (1/3 full), dark grey bar = 2 (2/3 full) and black bar = 3 (full); average monthly repletion index (RI) (dotted line). Numbers above bars (in parentheses) refer to the number of *C. carpio* analysed in each month for RI **d** Monthly changes in K_N of *C. carpio*, showing observed values (circles), mean (big circles) and standard deviations; water level variation in Canal Dos (continuous line) and the repletion index (RI) (dotted line). Numbers above (in parentheses) refer to the number of specimens analyzed every month.

was clearly identified through the end of our study (March 2011) using the length structure analysis. The lack of juvenile fish in the previous year indicated inter annual variability in recruitment success.

Age structure

The aging analysis using otoliths from 177 fish demonstrated that the population's age structure comprised age classes between 0 and 14 years. Two main groups were recognized as being the most dominant in the sample, the first from 0 to 1 years (n = 47) and the second comprised of fish aged between 6–9 years (n = 83) (Table 2). According to observed data of the monthly edge analysis asterici and the predicted model, fitted by the logistic periodic regression ($\hat{O}i = -1.075 + 1.038\ sin(2\pi Mi12 - 1) + 1.107\ cos(2\pi Mi12 - 1)$, $r^2 = 0.78$; $p > 0.05$), the temporal proportion of opaque zone depositions ($\hat{O}i$) for the monthly periods (Mi) reached maximum values once a year from May to July (Fig. 6).

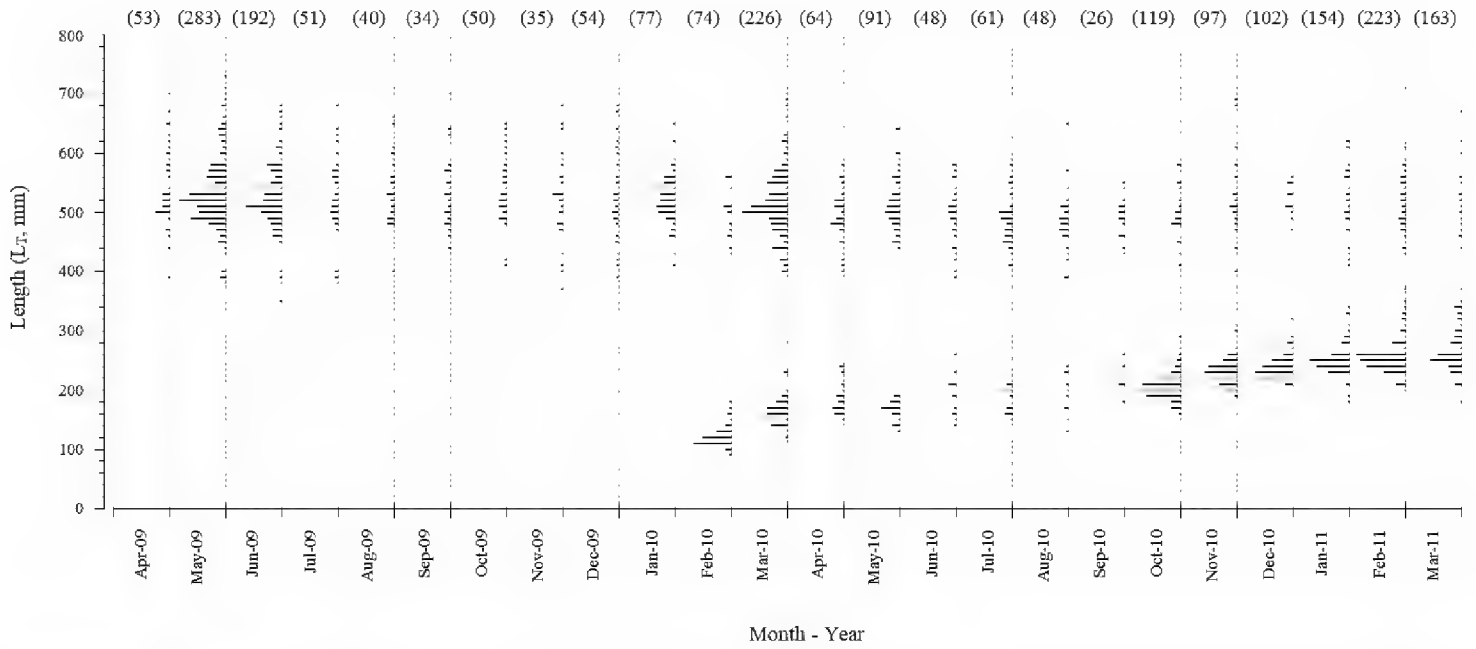

Figure 5. Monthly length-frequency distribution of the *C. carpio* population during the sampling period in the Ajó wetlands. In parentheses, the number of individuals captured in each month.

Table 2. Age length key (ALK) obtained for common carp *Cyprinus carpio* in the Ajó wetlands. Number of specimens analyzed (n = 177), discriminating the age assigned for a particular length category.

L_T (mm)	***Cyprinus carpio* age**														
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
150	3	1													
200	17	6													
250	7	7	1												
300	1	3													
350		1	4	1											
400		1	3	3	1	1									
450				6	1	1		1							
500				1	2	3	5	6	6	4					
550				1			5	6	8	3	1				
600					1	1	5	2	5	5		1		1	
650					1		1	2	6	1	2	3			1
700							2	1	2	6	4		1		1
750										1					

The relative strength of the annual cohorts of *C. carpio* in the population obtained by back-calculation based on population age structure, showed that an extraordinarily strong recruitment occurred during years of high annual precipitation, specially 2001–2002, while only weak cohorts were derived from years when rainfall was low (Fig. 7a). The regression between these variables from 2001 to 2009 (Fig. 7b) was portrayed by a positive lineal relationship ($y = 0.0225x - 15.713$; $r^2 = 0.79$), demonstrating that the *C. carpio* recruitment dynamic in the region is indeed strongly regulated by the annual precipitation regime.

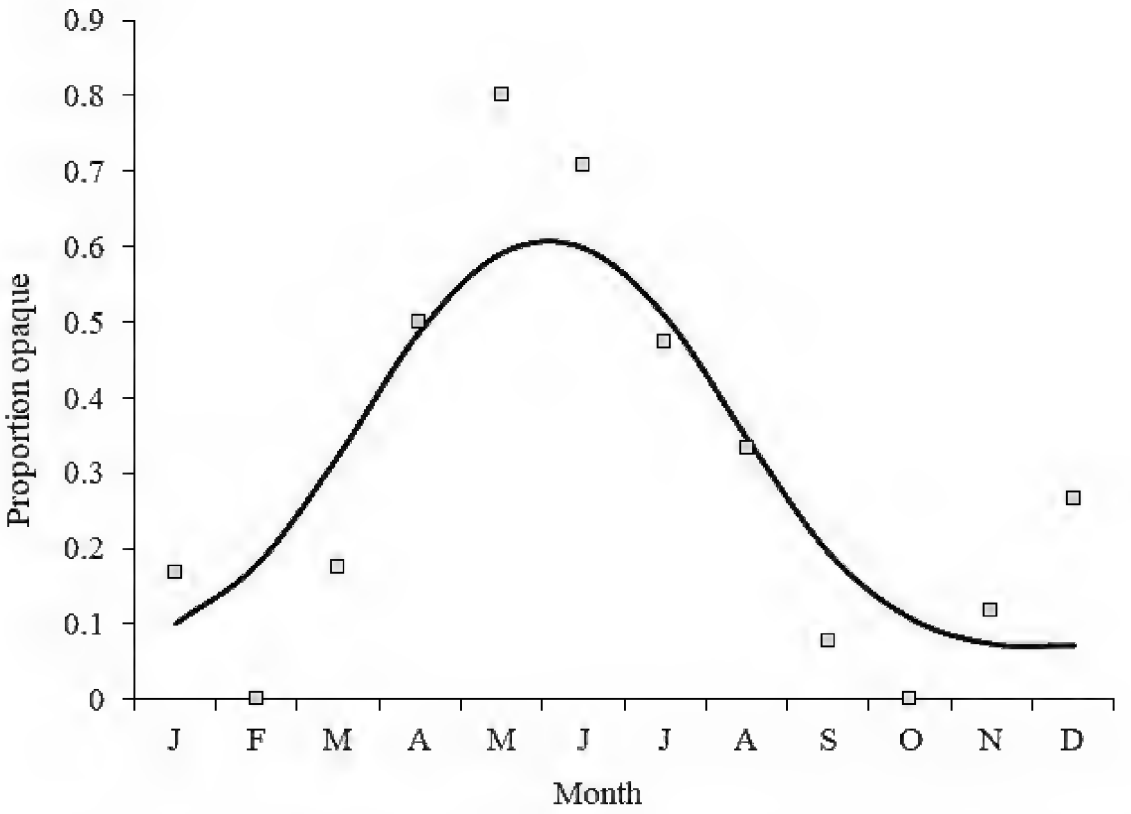

Figure 6. Monthly proportion of otoliths with an opaque zone on the margin for *C. carpio* in the Ajó wetlands (gray squares) and the predicted annual cycle of opaque deposition using logistic periodic regression (line).

Discussion

This study represents the first attempt to understand how *C. carpio* biological responses and population dynamics are synchronized with the yearly seasonality and modulated by multi-annual hydrological regime in temperate South American wetlands.

Here, as is the case elsewhere (e.g., Balon 1995; Stuart and Jones 2006; Penne and Pierce 2006), *C. carpio* spawning occurs between spring and summer when water temperature exceeds 15 °C and when shallow vegetated areas are available (Horvath 1985; Sivakumaran et al. 2003; Smith and Walker 2004; Winker et al. 2011). In the Ajó wetlands, female GSI followed a predictable seasonal pattern but the frequency, timing and synchronization of spawning differed between years (Fig. 4a). Spawning appears closely related to water levels during spring with more extended spawning during flood years and more protracted and dispersed spawning frequency during drought years. This was consistent with research conducted in the wetlands in the Camargue in France (Crivelli 1981), the Guadalquivir in Spain (Fernández-Delgado 1990), Victoria (Sivakumaran et al. 2003) and Barmah forest in Australia (Brown et al. 2005).

Cyprinus carpio diet in the present study was consistent with omnivorous feeding mostly associated with the benthos as observed elsewhere (e.g., Sibbing 1988; Sidorkewicj et al. 1998; Colautti and Remes Lenicov 2001; García-Berthou 2001). Feeding activity was related to the water level, reaching maximum values during HWPs, suggesting that adult *C. carpio* not only undertook lateral movements into recently inundated areas for spawning but also for access to new food resources. During low water levels, *C. carpio* were restricted to the C2 area where feeding opportunities were

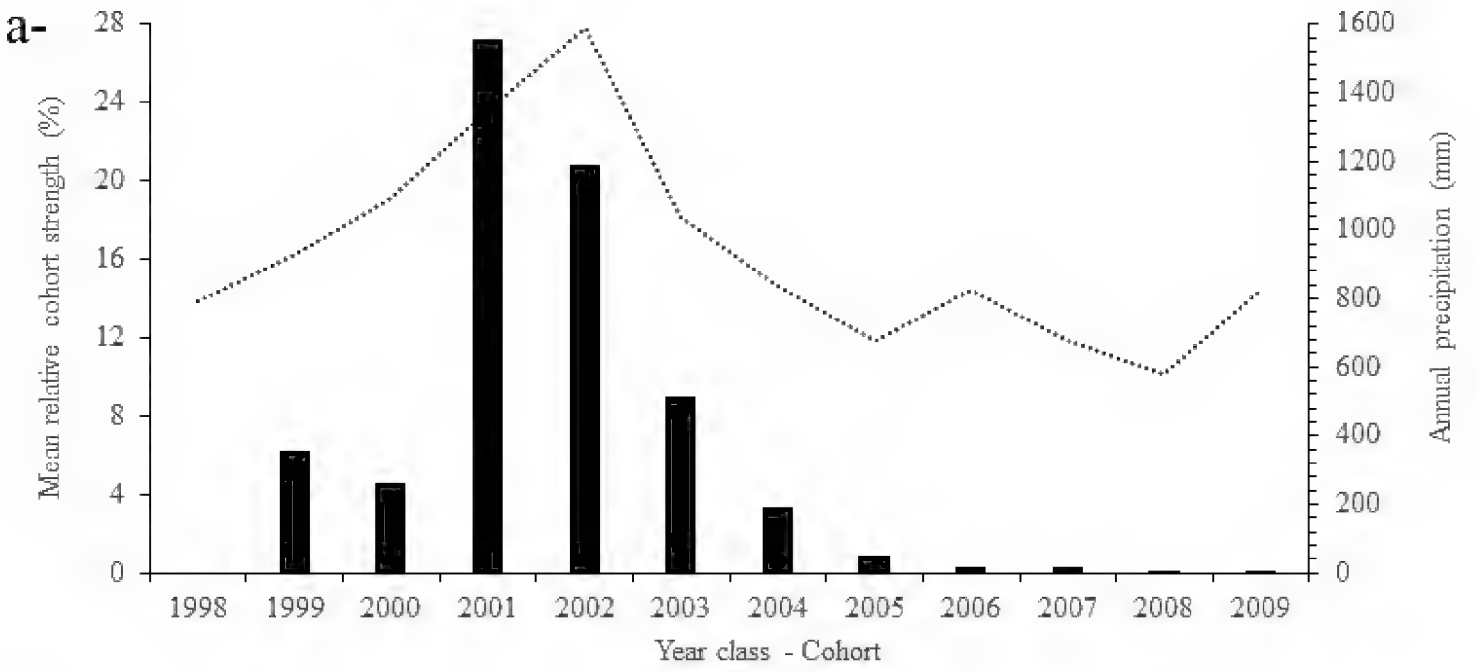

Figure 7. a Mean relative cohort strength (%) of *C. carpio* in the Ajó wetlands from 1998 to 2009 and annual precipitation in the Pampean region for the same time period (dotted line) **b** Regression between the annual precipitation of the Pampean region and the mean relative cohort strength (%) from the *C. carpio* population in the Ajó wetlands from 2001 to 2009. Dotted line indicates the model fitted to the dataset.

limited. Such observations are reinforced by the RI and DF% analysis which showed that *C. carpio* fed more intensely during HWP, in agreement with similar results showing the dependence of feeding activity on the hydrological regime (Jones and Stuart 2009; Daniel et al. 2011; Taylor et al. 2012). The influence of the habitat selection and water level was reflected by the variability of the repletion index, suggesting that food supply was at least partially dependent of entering into flooded habitats during regular high water levels. Increased feeding activity was reflected in body condition (K_N) which regressed positively with water level. On the other hand, during LWP, the gut content analysis also showed that feeding rate, and, by inference, food availability, was low.

During such periods *C. carpio* condition factor was the lowest documented during the study, probably associated with restriction to food resources in peripheral areas and the possible increase in intraspecific competition as the population was concentrated and restricted to C2. The connection between habitats facilitated by the HWP provided access to increased feeding opportunities that resulted in better condition, growth and increased recruitment success. As a result of the inherent climatic variability, the recruitment pattern in the Ajó wetland was more erratic than the regular patterns described in the Barmah Forest in Australia (Brown et al. 2005) and shallow lakes of South Dakota in USA (Weber and Brown 2013) but similar to the unstable interconnected aquatic environments of the Upper Mississippi River basin (Bajer et al. 2012).

Age data suggests that strong recruitment occurred during years of high annual precipitation (Fig. 7b). This study indicates that the pattern of regular and exceptional recruitment following rainfall and flooding events (Fig. 7a) is supported by age structure data which demonstrates that the population is dominated by individuals between 7 and 9 years of age, which is likely a result of strong recruitment during the exceptional flooding in 2002 (Scarpati and Capriolo 2013; Colautti et al. 2015). *Cyprinus carpio* are periodic life-history strategists (Winemiller 1992; Winemiller and Rose 1992) that, as a result of their long life span and high fecundity (King et al. 2003; Bajer and Sorensen 2010; Weber and Brown 2013), are able to overcome recruitment limitations during unfavorable years by maximizing their reproductive output when conditions are favorable. This storage effect (Warner and Chesson 1985) has also facilitated the persistence of *C. carpio* population in Ajó wetlands where weak annual recruitment and long starvation periods associated with regional droughts are compensated by strong recruitment during wet years.

This study demonstrated that increasing water levels promoted lateral migrations of *C. carpio* into peripheral habitats to take advantage of the network of small creeks as a nursery area, predation refuge for juveniles, and as a spawning and feeding grounds ground for adults. In addition, macro-scale climatic events strongly modulate *C. carpio* population dynamics in the Ajó wetlands, with wet and dry years enhancing and restricting recruitment respectively. We conclude that the *C. carpio* life-history in relation to climatic conditions has relevance for the control of this species in the Pampean wetlands. Human demands for water have resulted in the increased construction of infrastructure and land use changes to support agricultural expansion in the Pampean wetlands (Baldi and Paruelo 2008; Gras 2009). Water infrastructure development in the Pampean plain could represent a major driver of *C. carpio* persistence and dispersal because man-made channels and reservoirs could provide suitable habitats during prolonged drought periods for the persistence of *C. carpio* (as observed in C2) and could act as stepping stones enhancing species dispersal when these environments become connected during large flood periods. Management and control strategies for this invader should therefore incorporate hydrological variability by promoting intensive removal campaigns during dry years when populations are dominated by large fish confined in remnant waterbodies and, during wet years *C. carpio* harvest fisheries should be promoted to reduce population density when increased connectivity is likely to facilitate spread.

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